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Individual recognition in a wild cooperative mammal using contact calls

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Many of the mechanisms advanced to explain the evolution of intraspecific cooperative behaviour, such as reciprocity or social prestige, hinge on an animal's ability to recognize individual group members. However, 'true' individual recognition, between adult group members, has never been demonstrated in a cooperatively breeding bird or mammal species. We tested whether a wild cooperative mammal, the dwarf mongoose, *Helogale parvula*, could recognize individual group members from their vocalizations. We provided test subjects with a large, desirable food item and then simulated the approach of another group member using playbacks of its contact calls. Mongooses were more vigilant after hearing the calls of individuals of higher rank than themselves (that could steal their food) compared with individuals of lower rank than themselves (that could not). We showed that the mongooses were not simply responding to age-related cues that conveyed potential information on rank, and provide some evidence that they were associating the unique characteristics of the call with an individually specific characteristic of the caller (i.e. its relative rank). We conclude that dwarf mongooses exhibit 'true' individual recognition, and this finding supports the potential validity of mechanisms that rely on individuals monitoring the behaviour of others to explain the evolution of cooperative behaviour.
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Many of the mechanisms advanced to explain the evolution of intraspecific cooperative behaviour hinge on an animal's ability to recognize individual group members. Reciprocity (Trivers 1971; in which individuals exchange help) and social prestige (Zahavi & Zahavi 1997; in which individuals accrue status from helping) cannot exist unless animals are able to keep track of the behaviour of specific individuals. Similarly, the punishment or bribing of noncooperators, which underlies the strategies of 'pay to stay' (Gaston 1978; Kokko et al. 2002) or 'pay to breed' (e.g. Reyer 1990; Creel & Waser 1991), relies upon an animal's ability to recognize and monitor the cooperative contributions of other individuals. Likewise, indirect reciprocity by image scoring (Nowak & Sigmund 1998), in which individuals assess interactions between third parties, requires sophisticated recognition of multiple individuals. Although cooperative behaviour can exist in the absence of individual recognition, models show that the presence of individual recognition greatly facilitates its evolution (Hammond & Axelrod 2006). Despite this, 'true' individual recognition, between adult group members, has never been demonstrated in a cooperatively breeding bird or mammal species.

Individual recognition, which consists of one animal identifying another by its individually distinctive characteristics (Dale et al. 2001), has been reported in a wide range of taxa (Tibbetts & Dale 2007). However, in many of these instances it remains unclear whether the animal is identifying a single individual or has simply learned to associate the individual's unique and distinctive characteristics with a class of individual (e.g. one of my neighbours, one of my rivals, one of my offspring). When an animal genuinely associates an individual's cues with only one specific individual it is exhibiting 'true' individual recognition (Beecher 1989; Tibbetts & Dale 2007); and it is 'true' individual recognition that is required if members of social groups are to monitor one another's cooperative behaviour.

There is considerable debate over the best way to define and identify 'true' individual recognition. Some researchers believe that it is necessary to demonstrate that an animal can recognize multiple individuals within a given class (Thom & Hurst 2004) while others suggest that it is sufficient to show that the animal can recognize a single individual (provided the individual is unique to its class; e.g. a mate in a monogamous pair; Tibbetts et al. 2008). Other researchers argue that the whole concept of 'true' individual recognition is of limited value because the inherent difficulty of

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identifying an animal's perceptions makes it virtually impossible to test (Steiger & Muller 2008). In this study we follow the definition provided by Tibbetts & Dale (2007) which asserts that in order to demonstrate 'true' individual recognition it is necessary to show that the animal has not only learned the distinctive characteristics of the signaller (such as its calls) but also associates these with information that is unique to the signaller (rather than with class-specific information; Tibbetts & Dale 2007).

Such 'true' individual recognition has been well documented in primates (e.g. captive chimpanzees, *Pan troglodytes*, can select pictures of individual vocalizers after hearing their calls; Kojima et al. 2003) but demonstrating it in other taxonomic classes has proven much more difficult. Nevertheless, it was achieved for paper wasps, *Polistes fuscatus*, by demonstrating that the wasps associate the facial characteristics of nestmates with the nestmate's specific position in the dominance hierarchy (Tibbetts 2002; Tibbetts et al. 2008) and for hooded warblers, *Wilsonia citrina*, by showing that the birds associate the songs of specific neighbours with particular territories (Godard 1991). That 'true' individual recognition has never been demonstrated in a cooperatively breeding species may simply reflect the difficulty of devising appropriate experiments (Steiger & Muller 2008; Townsend et al. 2012) or that studies on these species have focused on kin and group recognition. However, we cannot dismiss the possibility that members of cooperative groups are not able to recognize one another, invalidating many of the proximal mechanisms that have been proposed for the evolution of cooperation.

If cooperative species are to monitor the helping behaviour of other individuals, they need to be able to recognize helpers even when visibility is reduced by vegetation or lack of proximity. Audio signals provide the ideal means and cooperative species are known to utter special vocalizations when performing cooperative behaviours, such as the provisioning call given when feeding young (e.g. McDonald et al. 2008) or the 'watchman's song' (Wickler 1985) voiced by sentinels as they guard the group from predators (Manser 1999; Kearn & Radford 2013). We know that group members monitor these vocalizations (altering their own behaviour in response; e.g. Manser 1999; Hollen et al. 2008) but it is unclear whether they also use them to identify helpers.

Many studies have shown that the vocalizations of cooperative species are individually distinctive (Rasa 1986; Payne et al. 1988; Sharp & Hatchwell 2005; McDonald et al. 2007; Schibler & Manser 2007), but we cannot assume that group members are able to discern these differences or associate them with specific individuals. This has been underscored by recent research on meerkat, *Suricata suricatta*, vocalizations (Schibler & Manser 2007; Townsend et al. 2010). Using a habituation–dishabituation playback experiment, McDonald (2012) showed that captive noisy miners, *Manorina melanocephala*, can discriminate between the mobbing calls of different individuals but it remains unknown whether the species uses this ability. Although studies have confirmed that cooperative species show class-level recognition, of kin or group members (Payne et al. 1988; Price 1999; McDonald & Wright 2011; Leclaire et al. 2013), 'true' individual recognition, apart from the recognition of offspring (Muller & Manser 2008) or the group's dominant female (Reber et al. 2013), remains unverified. In an effort to remedy this, Townsend et al. (2012) devised a novel experiment that showed that meerkats increase their vigilance when played a single individual's calls from two different locations. This suggests that the meerkats recognize the incongruity and thus the uniqueness of the call. However, it does not show that they associate the calls with specific individuals.

In this study we examined whether a cooperative mammal, the dwarf mongoose, *Helogale parvula*, exhibits 'true' individual recognition by testing whether wild dwarf mongooses associate the contact calls of individual group members with the caller's relative rank.

Dwarf mongooses are small carnivores that live in close-knit groups of 3–30 individuals. The alpha pair largely monopolizes breeding (Keane et al. 1994) but all group members assist in pup rearing (Rood 1978) and sentinel duty (Rasa 1986). Group members show a linear dominance hierarchy which, although correlated with age, is labile (Creel et al. 1992). Females are the philopatric sex and males exhibit delayed dispersal (Rood 1990). The mongooses forage together by day, maintaining group cohesion using individually distinctive and consistent contact calls (Marquardt 1976; Rasa 1986). They feed on arthropods and the occasional small vertebrate and, when food is scarce during the winter dry season, they steal prey from lower-ranking group members. A mongoose intent on stealing growls before commandeering the victim's foraging hole or snatching a large prey item from its mouth. Subordinates offer little resistance although those in possession of a particularly large item usually try to flee.

Capitalizing on this stealing behaviour, we provided test subjects with a large, desirable food item and documented their reactions to playbacks of the contact calls of socially subordinate and dominant group members. We predicted that if dwarf mongooses can recognize specific individuals from their vocalizations they will respond apprehensively to the contact calls of individuals of higher rank than themselves (that can steal their food) but ignore the contact calls of individuals of lower rank than themselves (that cannot).

METHODS

Study Population

We collected the data at Phuza Moya Private Game Reserve in northeastern South Africa (24°16′10″S, 30°47′46″E) between March and August 2012. Details of the study site's vegetation and climate are provided in Sharpe et al. (2010 electronic supplement). The study population consisted of four wild groups of dwarf mongooses (group sizes = 12, 13, 18, 18) habituated to an observer walking within 1–2 m. Because we have monitored the study population since 2006, the birth dates of most group members were known to within a few days, and all individuals were uniquely marked using Garnier Nutrisse hair dye (applied with a long-handled paintbrush as they were sunning). Only nonalpha adults (i.e. older than 1 year) were included in this study. Our methods were approved by the University of Stellenbosch's ethics committee and conform to the laws of South Africa.

Dominance Rank

To quantify dominance rank, we used critical incident sampling to document displacements at a resource (i.e. food, water or sunning sites), overt aggression or submission (i.e. uttering submissive vocalizations when grooming or approaching another group member; Rasa 1977). We used a handheld computer (Psion organiser II; model LZ64) to record the identity and role of the participants for 1186 dyadic interactions (range 177–432 per group).

To calculate ordinal dominance rank for all individuals, we used the I&SI method (de Vries 1998). For each of the four groups we compiled a 'win/lose' matrix which listed an individual's 'wins' (or assertions of dominance) beside its row name, and its 'losses' (submissions) under its column name (Fig. 1). An individual was considered dominant to another group member if its 'wins'

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(a)

Group member	KF6	KM2	KM4	KF44	KM36	**KM39**	KM58	KF67	**KF61**	KM68	KF72	KM71	KM70	KM77	KM76	KM75	KM81	KM80	Total asserts
KF6		1	3	4	1	2		3	2	2			1		2	2			**23**
KM2			4	1	1	1	2	1		2	1								**13**
KM4	2			1	6	5	1	4	2	2		1	2	1			2	2	**13**
KF44			1		3			1	2		1	2			1			2	**13**
KM36				1		6	1			4	1	9	4	3	2	3	2	5	**41**
KM39					1		1	1		2		2	1	1	4	1	3	2	**19**
KM58								1	1	2					2		2	3	**11**
KF67									4	1			1	4	2	2	2	5	**21**
KF61										3	3		2		2		1	1	**12**
KM68								1	1			5	1	2	6	2	2	3	**23**
KF72												2	2	1		1	5	2	**13**
KM71										2			3	3	1	1		3	**13**
KM70															1	1	1	2	**5**
KM77															6	5	3	8	**22**
KM76														2		4		8	**14**
KM75														3	1		7	5	**16**
KM81																		6	**6**
KM80																	1		**1**
Total submits	**2**	**1**	**8**	**7**	**12**	**14**	**5**	**12**	**12**	**20**	**6**	**21**	**17**	**20**	**30**	**22**	**31**	**57**	**248**

(b)

Group member	EM34	EF5	EF22	EM38	EM39	**EF42**	EM47	EM50	EF53	EM58	EM60	EM61	Total asserts
EM34		4	6	4	4	4	3	3	2	4	3	7	**44**
EF5			4		2	1		2	1			2	**12**
EF22				2	2	3			3	1	2	3	**16**
EM38					21	1	3	2	4		6	12	**49**
EM39						3		4	5	4	1	2	**19**
EF42					1		1	1	2	1		3	**9**
EM47								2	2	1	1	8	**14**
EM50									2		1		**3**
EF53										1	2	3	**6**
EM58												1	**1**
EM60												2	**2**
EM61											2		**2**
Total submits	**0**	**4**	**10**	**6**	**30**	**12**	**7**	**14**	**21**	**12**	**18**	**43**	**177**

Figure 1. 'Win/lose' matrices for the four groups showing rank-related dyadic interactions. (a) Koppiekats group; (b) Ecthelion group; (c) Halcyon group; (d) Bugbears group. Rows show the number of interactions in which the individual asserted dominance; columns show the number of interactions in which the individual behaved submissively. Individuals used in the same-sex experiment have their column names shaded (large area of shading = male experiment; small area of shading = female experiment). Individuals used in the same-age experiment have their row names shaded (triplets grouped in boxes). Test subjects' names are shown in bold type.

outnumbered its 'losses' in interactions between the two. We then rearranged the order of individuals within the matrix to reflect these dyadic relationships. Pairs with an unknown relationship (no encounters observed) or tied relationship ('wins' equalled 'losses') were ordered based on the relative number of group members each partner dominated (except where this generated inconsistencies; de Vries 1998). The linearity of the resultant hierarchies did not show any reversals (i.e. A > B and B > C but C > A). For each group, we ascertained the probability of linearity occurring by chance using the method outlined in Appleby (1983).

Sound Recordings

To obtain recordings of vocalizations for use in the playback experiments (and for acoustic analysis), we accompanied the mongooses during their morning foraging sessions and recorded the contact calls of all adult, nonalpha group members ($N = 40$) using a Sennheiser directional microphone (ME66/K6) and a Marantz Professional portable recorder (PMD670). At least six calls were obtained from each individual (normally over several mornings) from a distance of 1–2 m. We measured call volume using a

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(c)

Group member	HM2	HF5	HM52	HM50	HF33	**HF37**	HM51	**HM40**	HM45	HF41	HM48	HF47	HF46	HF54	HU55	HU56	HU57	HU58	**Total asserts**
HM2		7	4	22		6	9	7		3	5	7	5	8	1	3	2	4	**93**
HF5	3		7	16	1	4	4	2		4	2	1	6	5	1	3	1		**60**
HM52				2		1	2	1			3	3	4	8			1		**25**
HM50						7	10	3	2	2	3	5	5	8				2	**47**
HF33						2				1		3	1		1		2	1	**11**
HF37			1	2	1		2	5	1	6	2	12	8	7		2	4	4	**48**
HM51								1		1	2	3	2	6		5	1	6	**27**
HM40									2	1	2	4	4	9		1		1	**24**
HM45										2			1		1	1	1	2	**8**
HF41												4	6	4				1	**15**
HM48						1						5	2	8	2	1	3	3	**25**
HF47											1		7	8		1	2	4	**23**
HF46														1	1	1			**3**
HF54															1		1	4	**6**
HU55																	1	3	**4**
HU56																	1	4	**5**
HU57																		1	**1**
HU58																			**0**
Total submits	**3**	**7**	**12**	**42**	**2**	**21**	**27**	**19**	**5**	**18**	**20**	**47**	**51**	**72**	**8**	**18**	**20**	**40**	**432**

(d)

Group member	BM3	BF10	BF17	BM18	**BF22**	**BM33**	BM32	BF25	BM35	BF38	BM44	BF46	BF50	**Total asserts**
BM3		3	4	2			5	1	10	1		5	7	**38**
BF10			10	6	9	1	2	11	6	3	1	3	8	**60**
BF17				1	11	2	1	17	2	11	1	1	7	**54**
BM18						3	6	1	5			2	4	**21**
BF22							2	13	1	3	1	1	4	**25**
BM33							2		2					**4**
BM32					1	1		3	4	1	7	8	5	**30**
BF25									1	5		2	8	**16**
BM35										3	1		7	**11**
BF38											1	6	12	**19**
BM44												1		**1**
BF46													1	**1**
BF50														**0**
Total submits	**0**	**3**	**14**	**9**	**21**	**7**	**18**	**46**	**31**	**27**	**12**	**29**	**63**	**280**

Figure 1. (*continued*).

Velleman sound-level meter (model DVM805; range 30–100 dB; 1.5 dB accuracy) positioned 1.5 m from the caller.

To examine whether mongoose contact calls varied with caller age, we created spectrograms of the contact calls of 38 known-aged, nonalpha adults using Adobe Audition 2.0. We then measured the fundamental frequency (Hz) of each individual's call and plotted this against its age (in days) at the time of the call recording.

To create playback recordings for use in the experiments we used Adobe Audition 2.0. After removing the background noise from recorded contact calls, we selected six good-quality vocalizations from each target individual and constructed a 6 s playback recording by separating each of the calls with 0.8 s of silence (i.e. the natural calling rate of a briskly walking mongoose). The amplitude of each call was modified so the volume increased slightly over the sequence (to simulate the approach of the caller) and the volume of the playback was tested with the sound-level meter (at a distance of 1.5 m) to ensure a playback amplitude of 40–45 dB (the natural volume).

Playback Experiments

To test whether individual mongooses were able to recognize higher and lower-ranking group members from their contact calls alone, we undertook two playback experiments. We conducted all experiments during the dry winter months when natural prey was

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scarce. In both playback experiments, we accompanied the foraging mongooses on foot and presented the test subject with half a mouse when it was foraging away from other group members. Mice were purchased frozen from a local pet shop for this purpose. The subject usually carried the item to an isolated location and we began videoing its behaviour (using a Sony Handycam DCR-SX60E) only after it had settled down to eat. We filmed for 10 s prior to the playback (to obtain baseline vigilance data) and continued for 5 s after the playback finished. The 6 s playback featured the contact calls of a mongoose from the test subjects' group and was broadcast from a Marantz Professional portable recorder (PMD 670) held at mongoose height, 1.5 m from the subject. For each test subject we conducted two trials, one featuring the contact calls of an individual dominant to the subject and the other featuring the contact calls of an individual subordinate to it. We randomized the order in which we played the different calls, allowing 3–4 days to elapse between trials.

In the first experiment (the 'same-sex' experiment) we used callers of the same sex as the test subject because rank-related interactions are more frequent between same-sex group members and two-thirds of natural food-stealing incidents occur between same-sex individuals despite an even sex ratio ($N = 596$ thefts; L. Sharpe, unpublished data). One male and one female subject were selected from each group based on their position in the hierarchy: i.e. the group contained at least one same-sex group member of lower rank and one of higher rank (excluding the alpha pair). In one group, the only qualifying male proved unfilmable (always retreating underground to eat his mouse) resulting in seven test subjects (four females and three males; Fig. 1).

To control for the possibility that the mongooses used age-related vocal cues to identify a caller's rank, we undertook a second playback experiment (the 'same-age' experiment) in which we used callers that were the same age as the test subject, regardless of their sex. Within groups, we identified sets of adult 'triplets' (i.e. three individuals from the same litter or born within 2 months) and nominated the middle-ranking triplet as the test subject and the other two as dominant and subordinate callers, based on their rank. In total, our study groups contained seven sets of triplets (four in one group, two in a second group and one in a third group; Fig. 1). None of these seven test subjects (five males and two females) had acted as test subjects in the earlier experiment, and although four individuals provided calls for both the same-sex and same-age experiments, we created new playback recordings (constructed from hitherto unused vocalizations). Furthermore, two of these callers changed role, acting as a subordinate caller in the same-sex experiment and a dominant caller in the same-age experiment. (Fig. 1 identifies the individuals that participated in the experiments, and their positions within the group's hierarchy.)

Video recordings of the experiments were analysed frame-by-frame (25/s) using K-Multimedia Player (R2). We counted the frames to ascertain the duration of the test subject's vigilance bouts (i.e. pausing chewing to look towards the speaker or scan the surroundings). We documented the duration of vigilance for the 10 s period prior to the playback (to ascertain baseline vigilance) and for the playback response period (i.e. the duration of the playback and 5 s after). Statistical analyses were performed using Statistica 10 (Statsoft, Tulsa, OK, U.S.A.). Zero vigilance values were entered as 0.0001 s so that they were not excluded from statistical testing. Because the data were not normally distributed (Kolmogorov–Smirnov test), we used Wilcoxon exact signed-ranks tests to compare the vigilance of test subjects when played subordinate and dominant vocalizations, for both experiments. Median values are presented ±25% interquartile ranges.

RESULTS

All four study groups exhibited a clear, linear dominance hierarchy (Fig. 1). The probability of this occurring by chance was <0.001 in all four groups (Appleby 1983).

There was a significant negative correlation between the fundamental frequency of dwarf mongoose contact vocalizations and age, with older adults producing calls of a lower pitch than younger adults (Pearson correlation: $r_{37} = -0.58$, $P < 0.001$; Fig. 2).

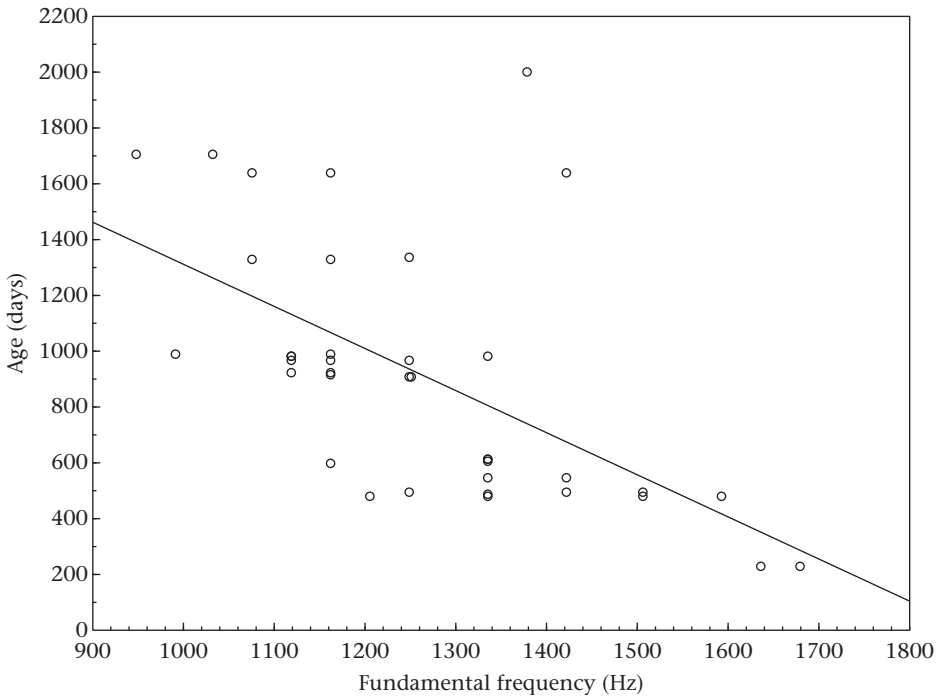

Figure 2. The relationship between age and fundamental frequency (Hz) of contact calls in adult dwarf mongooses.

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When consuming a large food item, test subjects became significantly more vigilant after hearing the contact calls of a higher-ranking group member as compared with a lower-ranking one. In the same-sex experiment mongooses interrupted eating to scan their surroundings for 2.1 ± 1.2 s in response to a more dominant individual's calls compared with 0.8 ± 0.0 s for a subordinate's ($W = -21.00$, $N = 7$, $P = 0.031$; Fig. 3). Similarly, although the mongooses never interrupted their meal in response to the calls of a lower-ranking, same-aged peer, they spent 2.9 ± 1.1 s vigilant after hearing the calls of a higher-ranking, same-aged peer ($W = -21.00$, $N = 7$, $P = 0.031$; Fig. 3).

Baseline levels of vigilance (measured immediately prior to the playback) did not vary between the two test conditions (i.e. subordinate versus dominant calls) for either experiment (same-sex: $W = 6.00$, $N = 7$, $P = 0.375$; same-age: $W = -4.00$; $N = 7$, $P = 0.625$). This shows that the experimental results were not caused by extraneous factors, such as variations in perceived predation risk.

DISCUSSION

Dwarf mongooses clearly discriminated between the contact calls of different group members. As predicted, they responded with greater vigilance to the vocalizations of animals that were dominant to themselves as compared with animals that were subordinate (Fig. 3). This suggests that dwarf mongooses use contact calls to identify individual group members. However, it is possible that the mongooses were exhibiting class-level recognition rather than 'true' individual recognition, using one of two possible means. First, the test subjects may have classified callers as high-status or low-status group members based on rank-related cues within the calls. Alternatively, subjects may have recognized the unique characteristics of the calls, but associated each 'known' call with a category of group member (i.e. 'dominant to me' or 'subordinate to me') rather than with a specific individual. Only by examining the findings more closely can we ascertain which strategy the mongooses were adopting.

Although the presence of a dominance hierarchy suggests that group members are able to recognize one another and recall one another's rank, this is not necessarily the case. Linear dominance hierarchies can form in the absence of individual recognition (Wiley 2012) if individuals respond directly to overt differences in one another's competitive ability (as evidenced by body size, for example) or status symbols (e.g. tail length, bill colour). So do dwarf mongooses' contact vocalizations contain cues that correlate with the caller's competitive ability and hence rank?

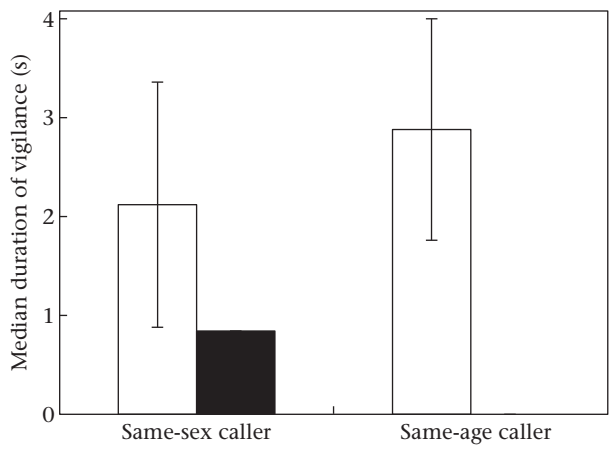

Figure 3. The median duration of vigilance shown by dwarf mongooses consuming prey in response to the contact calls of a higher-ranking group member (white bars) and a lower-ranking group member (black bar), using calls from same-sex or same-age individuals. Error bars show 25% interquartile ranges.

An obvious candidate would be the vocal traits associated with body size (e.g. fundamental frequency; Ey & Fischer 2007). However, size is not a reliable predictor of status in dwarf mongooses (body mass accounts for only 14% of variation in rank; Creel et al. 1992) so the mongooses could not have been using size-related vocal traits to identify a caller's rank. In contrast to size, age is positively correlated with rank in dwarf mongooses (accounting for 69% of variance in rank; Creel et al. 1992) and age causes changes to the vocal apparatus. Both vocal fold length and vocal tract length increase with age (Ey & Fischer 2007), altering the acoustic characteristics of vocalizations (Ryan & Burk 1974). In primates, older individuals consistently produce longer calls of lower fundamental frequency (Ey & Fischer 2007) and such differences in call pitch are known to be used by other species when discriminating between vocalizers (e.g. Ceugniet & Izumi 2004). When we plotted the fundamental frequency of the mongooses' contact calls against age we found a significant negative correlation (Fig. 2). As a consequence, it is possible that the test subjects in the same-sex experiment were responding simply to the pitch of the playback calls: older, deeper-voiced callers would pose a potential threat of kleptoparasitism, while younger, high-pitched callers would not. Such categorization may have been facilitated by the relatively large differences in age (and status) that existed between dominant and subordinate callers in this experiment (see Fig. 1's column names for the relative rank position of callers).

To test whether this was the case we conducted the same-age playback experiment in which the dominant and subordinate callers were identical in age and hence their call pitch did not differ systematically. However, the test subjects still responded as predicted to the vocalizations, increasing their vigilance after hearing the dominant's contact call and showing no vigilance in response to the subordinate's call (Fig. 3). Clearly, the mongooses were not simply cueing on age-related differences in the vocalizations.

It is possible that some other vocal trait allowed test subjects to identify the caller's status without actually identifying the caller itself. For example, high-status group members seemed to call more loudly than low-status individuals but, since we played all calls at the same volume, test subjects did not use call amplitude to categorize callers. Also, the same-age experiment minimized the potential impact of any rank-related vocal cues because the dominant and subordinate callers were very close in rank (their adjacent positions within the hierarchy are shown in Fig. 1's row names). We also used 'neutral' vocalizations that merely simulated the approach of a group member. Contact calls never feature in the species' repertoire of agonistic behaviours and are therefore far less likely to convey information about aggressiveness or status than calls designed to intimidate, such as the growl used during foraging competition.

Further evidence that the mongooses were recognizing the unique characteristics of the contact calls (rather than homing in on rank-related cues) was provided by the test subjects' reactions to the two individuals that acted as subordinate callers in the same-sex experiment but as dominant callers in the same-age experiment. In these cases, different test subjects responded in different ways (although always as predicted) to the calls of the same animal, solely because of differences in their own rank. This makes it clear that there was nothing intrinsically 'high status' or 'low status' about the vocalizations themselves.

Based on this evidence, it appears highly likely that the mongooses were recognizing the unique characteristics of the vocalizations. Nevertheless, it is possible that they then associated these known calls with categories of group member (i.e. 'dominant

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to me' or 'subordinate to me') rather than with specific callers. Although it is clearly beneficial for an individual to know the rank of other group members to avoid potentially dangerous conflict, recognizing multiple individuals requires complex associative learning skills (Wiley 2012). If the same benefits can be attained using a simpler mechanism (e.g. learning to lump callers into just a couple of categories based on their rank), it is most unlikely that a species will exhibit 'true' individual recognition (Wiley 2012). There is considerable empirical evidence that the complexities of a species' recognition skills are commensurate only with its needs. For example, among closely related swallows, species that nest in colonies are able to recognize their own offspring but solitary nesters are not (Beecher et al. 1986). Similarly, penguins that rear their young in fixed nests use simpler cues to recognize their chicks than penguins that breed in shifting colonies where location is of no assistance (Jouventin & Aubin 2002). So do dwarf mongooses need to recognize individual group members, or is it sufficient for them to learn simply which vocalizations are associated with a potential threat and which are not?

Dominance rank in dwarf mongooses is not fixed and is strongly contested between same-sex group members (Creel et al. 1992). Rank-related fights between nonalpha individuals (particularly in females that queue for the alpha position) often result in injury, and rank reversals are not uncommon, usually occurring when a group member becomes sick, injured or loses weight relative to its competitors (L. Sharpe, personal observation). Given these circumstances, a dwarf mongoose needs to be able to recognize individuals that are close to itself in rank so it can monitor their health and behaviour and respond rapidly to opportunities to improve its own rank. We would therefore expect dwarf mongooses to exhibit 'true' individual recognition of at least these group members, although the ability may not extend to include all group members, and categorization may be employed for individuals that are highly disparate in rank.

Evidence that the mongooses were indeed associating calls with specific callers (rather than with categories) was provided by the only test subject that failed to show vigilance after hearing the call of a higher-ranking, same-sex animal. In this particular trial, 2 weeks elapsed between our recording of the dominant animal's vocalizations and the playback experiment. During this time the dominant caller fell ill, visibly losing weight. Although she was still socially dominant to the test subject at the time of the playback experiment, 3 days after the experiment the test subject mounted a challenge and their ranks were reversed. It is evident from the test subject's lack of response to the dominant's contact call that she was not merely reacting to the call per se (which was recorded when the caller was healthy) nor associating the call with a simple 'more dominant than me' category. It appears highly likely that she was associating the call with the specific caller and using her current knowledge of the caller's ill health to assess her risk of kleptoparasitism accurately. Although this is only a single example, it clearly suggests that the mongooses are associating contact calls with specific callers.

In conclusion, we believe that our study provides convincing evidence that dwarf mongooses use contact vocalizations to identify individual group members. The playback experiments offer good qualitative evidence that the mongooses recognize the unique characteristics of group members' contact calls and associate these with individually specific information (i.e. relative rank) about the callers. To our knowledge, this is the first time that 'true' individual recognition has been demonstrated for a cooperatively breeding bird or mammal species. These findings support the potential validity of mechanisms that rely on individuals monitoring the helping behaviour of others to explain the evolution of cooperative behaviour.

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